



Unlocking the biogeochemical role of beaver in state-transition of landscapes in Yellowstone's northern range

Marjorie L. Brooks

Department of Zoology, Southern Illinois University, Carbondale, IL
mlbrooks@siu.edu

Abstract Extirpation of wolves from the Greater Yellowstone Ecosystem in the 1920s hypothetically triggered a trophic cascade in which browsers, released from wolf (*Canis lupus*) predation, over-browsed riparian zones. Eventually, vast meadow-wetland complexes transitioned to grass-lodgepole systems. By 1954, beaver (*Castor canadensis*) virtually abandoned the Greater Yellowstone Ecosystem. In 2000, Colorado State University established experimental dams with browsing exclosures for Long Term Research in Environmental Biology (LTREB) on three streams in Lamar Valley to compare hydrologic effects of pseudo-beaver dams and browsing on willow (*Salix* spp.) productivity and state transitions. In 2015, beaver began recolonizing the region. I investigated how the biogeochemical role of beaver versus their hydrologic influence affects the underlying mechanisms of state transition: nutrient cycling, productivity, and stream respiration. Analyses of the 2017 field samples show that beaver streams trend toward higher nutrient levels and higher variances than the LTREB sites. The data tentatively support the role of beaver as keystone species in state transitions, although more data are needed. The unexpected and late May notice from the NPS to obtain an independent research permit—approved late August—curtailed my 2018 research to a brief field bout in September. Analysis of 2018 samples is underway.

Introduction

Based on increased growth of riparian vegetation following the 1995 reintroduction of the wolf (*Canis lupus*), researchers hypothesized that wolf extirpation in the 1920s released elk (*Cervus elaphus*) and other ungulates from fear of predation in riparian zones (Ripple and Beschta, 2004, 2012; Painter et al., 2015). Subsequent over browsing led to degraded riparian vegetation and a state transition from productive meadow-wetland complexes to dry grasslands (Figure 1). A lively scientific debate continues about the relative influences on wetland recovery from the wolf-elk trophic cascade, overall declines in elk populations, effects of other browsers, and periodic drought events (Creel and Christianson, 2009; Kauffman et al., 2010; Beschta and Ripple, 2013;

Kauffman et al., 2013). The evidence for both sides of the debate has largely depended on mensurative field studies. Such observational and sampling studies carry tremendous ecological relevance but, because they are fundamentally observational, they face challenges from lack of replication, reproducibility, and strictly controlled reference sites.

Eighteen years ago, David Cooper and Tom Hobbs from Colorado State University established an experimental site for Long Term Research in Environmental Biology (LTREB) in the Lamar Valley, *Understanding controls on state-transition on Yellowstone's northern range*. To evaluate the effects of increased hydrologic delivery of groundwater and elk browsing, they installed a series of experimental dams at three stream sites with adjacent exclosures that prohibit brows-



Figure 1. Comparison of historic photos of Elk Creek in the Lamar Valley. In 1923, the beaver dam was more than 100 m long with a robust willow stand (Warren, 1926). The dam had drained and the willows were gone by 1954 (Jonas, 1955). By 2002, a grass and lodgepole pine community entirely replaced the willow-meadow complex. The black line marks the old dam location with the deeply incised stream in the foreground (From Wolf et al., 2007, Figure 8).

ing. The experimental dams mimic the influence of beaver (*Castor canadensis*). They and their students show that hydrologic changes, water availability, and drought regimes determine willow growth (Schook and Cooper, 2014) to a greater extent than elk grazing (Wolf et al., 2007; Marshall et al., 2013, 2014). In addition to hydrologic influences, the next logical step is to investigate the biological mechanisms by which beaver alter nutrient cycling, stream metabolism, or system productivity.

By the mid-1950s, beaver populations had declined precipitously throughout the Greater Yellowstone Ecosystem and virtually disappeared from the Lamar Valley (Persico and Meyer, 2013). Beaver apparently abandoned because of a combination of overbrowsing and drought events in the 1930s. Without beaver maintenance, spring runoff eventually breached their dams, which dramatically changed wetland-meadow hydrology (Wolf et al., 2007; Persico and Meyer, 2013). Beyond their hydrologic influences, beaver biologically facilitate ecosystem productivity by adding nutrients as feces and transferring woody debris into streams (Figure 2). Their activity enhances primary production, while promoting higher decomposition rates and nutrient regeneration (Johnston and

Naiman, 1987, 1990; Naiman et al., 1994; Klotz, 1998). For example, Naiman and Melillo (1984) found that nitrogen fixation in a stream riffle contributed 4.2% of the nitrogen, but in a similar reach dammed by beaver, fixation contributed 68% of the annual nitrogen budget (Naiman and Melillo, 1984). Although such benefits are well described, dynamic thresholds, chronology of changing system productivity, the magnitude of their influence, and separation of hydrologic from biologic mechanisms are not (arrows between compartments in Figure 2).

In the past, detection and investigation of the separate hydrologic and biologic processes provided by beaver were impossible because there were no beaver dams to compare to the experimental dams. Starting in 2015, however, beaver conveniently began colonizing streams, below or near the LTREB sites (Figure 3). LTREB research had not previously included nutrient assessments.

In 2015, beaver began recolonizing streams in the Lamar Valley. Beaver immigration presents an unprecedented opportunity in ecology to investigate several important questions about the interplay between the hydrologic and biologic mechanisms. Will

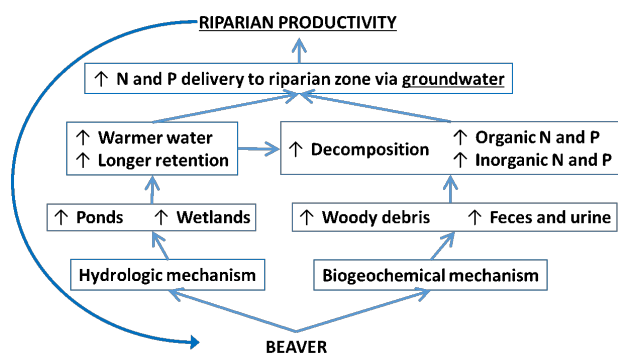


Figure 2. Conceptual model of beaver as keystone species in the state-transition of streams to wetland meadow complexes.

the recovery of systems be adequate to sustain viable beaver populations? Will productivity approach historical levels of productivity that can sustain beaver and many wetland-dependent species and fishes (Collen and Gibson, 2000; Hossack et al., 2015; Law et al., 2016)? What timeframe is required for their sustainability? The aims of this research are consistent with research needs for the Greater Yellowstone Ecosystem, which include studying willow recovery following wolf reintroduction.

Rationale and Significance

As in areas fertilized by salmon and river otters (Helfield and Naiman, 2001; Roe et al., 2010; Kominoski et al., 2015), I posit that biological feedback of nutrients, mediated by beaver, is critical to full system recovery. Unlike otters, beavers seldom defecate onshore. However, their biologic influence on nutrient levels within streams can reach riparian vegetation via surface flooding or lateral seepage of groundwater to the hyporheic zone. My preliminary data collected in 2015 and 2016 from newly established beaver ponds indicate higher N and P concentrations in groundwater beneath riparian zones adjacent to beaver dams than in experimentally dammed streams (Figure 4). If this pattern holds in further studies, it would represent a newly discovered mechanism by which alteration of nutrient dynamics within streams by beaver accelerates the transition from elk meadows lacking willows to beaver meadows with vigorous willow growth. This nutrient-driven process,

which occurs in tandem with greater surface flooding around dams and accompanying lateral seepage of groundwater, adds a novel parallel dimension to better-recognized hydrologic effects of beaver (Figure 2).

Research Questions

1. How do nutrient levels and cycling depend on the biological influence of beaver (i.e. active nutrient input) compared to analogous hydrologic alterations at the LTREB sites?
2. What effect does beaver presence have on ecosystem respiration and net primary production of streams compared to LTREB sites that lack beaver?
3. Do beaver contribute significantly to riparian willow and aspen productivity (e.g. shift in stable isotopic signatures)?

Coupling the LTREB monitoring with my biogeochemical sampling will allow greater understanding of these questions about ecosystem function and the trajectory of system productivity over time as beavers recolonize the Greater Yellowstone Ecosystem. The steps in the process of characterizing and testing beaver influence include sampling: (1) levels of nutrients and rates of nutrient regeneration and cycling in the streams (Hall et al., 2013; Kominoski et al., 2015; Hall et al., 2016), (2) nutrient levels in groundwater wells within the riparian zone, and (3) growth rates and nutrient levels in leaves of riparian vegetation (Ben-David et al., 1998; Hubbard Jr et al., 2010; Roe et al., 2010).

Methods

Samples were collected at five locations from 9–14 September 2018. I excluded the West Blacktail beaver site because it was abandoned some time before May 2017. Samples were collected 50, 10, and 5 m above the dam furthest upstream and 5, 10, and 50 m below the dam furthest downstream. Samples were transported from the field on ice, and stored frozen at -5 °C until analysis. Sample analysis from the 2018 season are currently being analyzed. Following thawing, samples are analyzed or

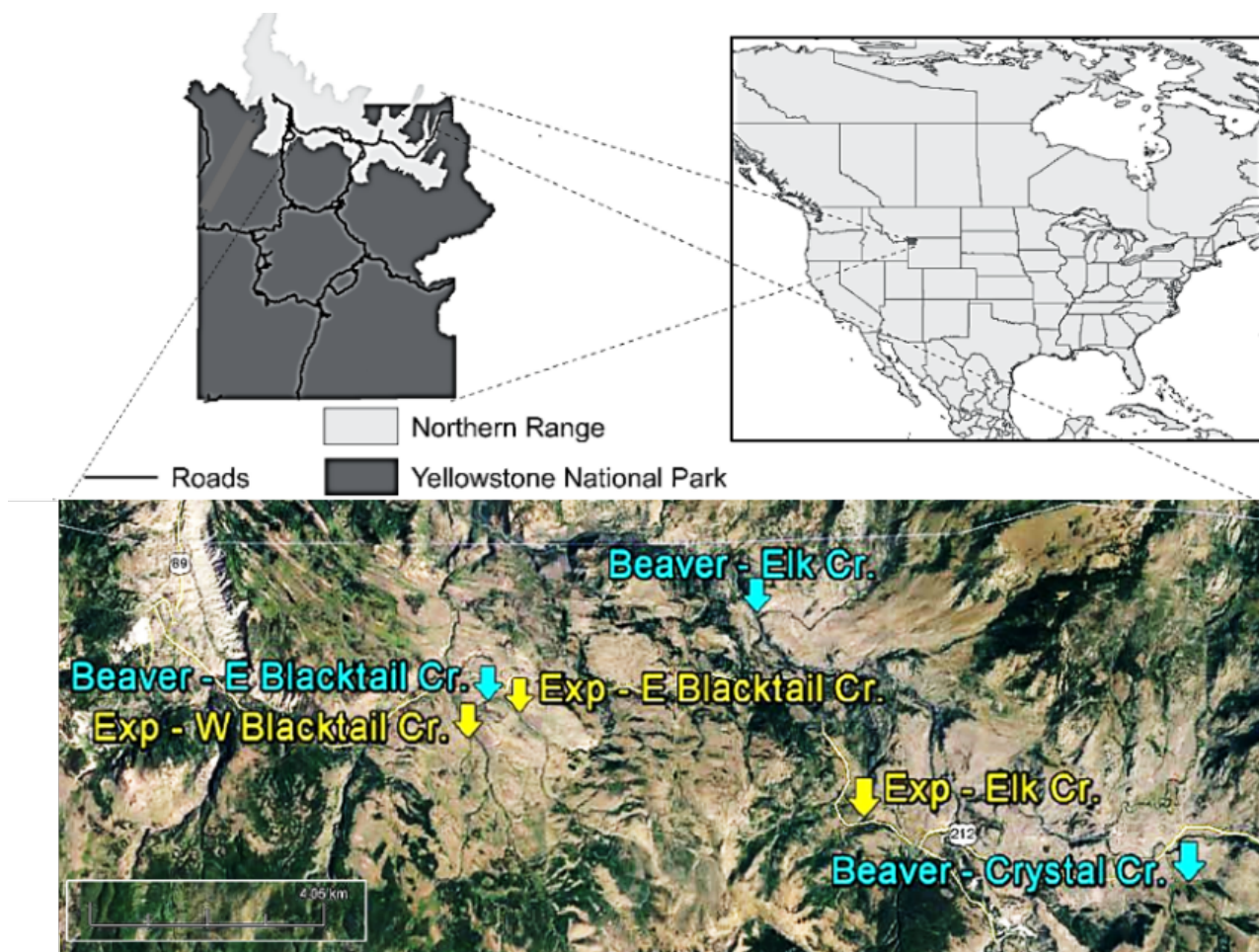


Figure 3. Locations of LTREB experimental dams (West Blacktail Creek, East Blacktail Creek, Elk Creek) and beaver dams (Crystal Creek, Elk Creek, East Blacktail Creek) (after Marshall et al., 2014)

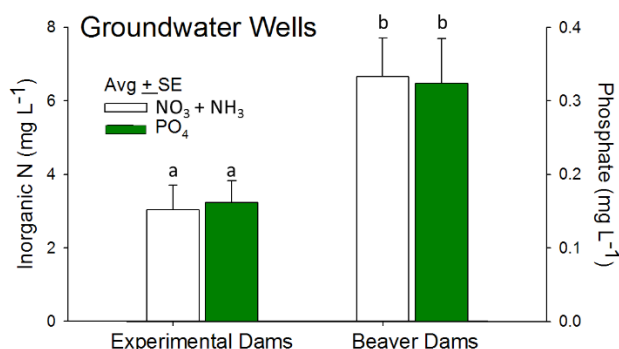
stabilized within 24 hours. Temperature, pH, conductivity, and dissolved oxygen are collected at each stream with appropriate probes (HQ40d, HACH multi-parameter meter). Similarly, field data are collected for gross primary production (GPP), ecosystem respiration rates (ERR), and organic carbon spiraling by two-station oxygen logging with modeled gas exchange and organic carbon spiraling. Aside from stable isotopic analyses, which are sent to the University of Wyoming Stable Isotope Facility, all other analyses are conducted in my laboratory at Southern Illinois University. Organic carbon spiraling is determined from particulate organic carbon (total dry mass minus ash-free dry mass of fraction $> 0.45 \mu\text{m}$) relative to dissolved organic carbon (fraction $< 0.45 \mu\text{m}$; catalytic combustion; Shimadzu TOC-VCSN). Nitrate

and phosphate are analyzed by ion chromatography (Dionex ICS 2000, method 300.0), total nitrogen by chemoluminescence (Shimadzu TOC-VCSN), and ammonia, nitrate, and total phosphorus by colorimetric analyses (Hach 5000 spectrometer) using EPA standard methods (P method 365.2, NH_3 method 350.2). Quality assurance and quality checks follow standard QA/QC protocols of duplicates, spikes, and external quality checks and external reference materials (APHA et al., 2005).

Statistical analyses

Statistical analyses include Bayesian network models for the strength of relationships in Figure 2 (Ayre and Landis, 2012; Raiho et al., 2015). For hypothesis testing of differences in system productivity be-

| Sample types (n per site) | Analytes or parameters |
|--|---|
| Stream (n = 6) and well waters (n = 7 to 12) | temperature, pH, conductivity, dissolved O ₂ , NO ₃ , NH ₃ , PO ₄ , total N, particulate & dissolved organic carbon |
| Willows (n = 6) | total P, total N, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, C:N, % C, % N |
| Stream metabolism (n = 1) | Whole stream respiration and organic carbon spiraling |

Table 1. Samples and data collection at field sites in 2018.**Figure 4.** Comparison of total inorganic nitrogen and phosphate collected in 2016 from groundwater wells adjacent to LTREB experimental dams and beaver dams shown in Figure 3 (Brooks, unpublished data).

tween undammed reaches, experimental dams and beaver dams, I use permutational multivariate analysis of variance (PERMANOVA; PRIMER software ver 7.0.11, PERMANOVA, 1.0.5; PRIMER-E; Anderson, 2001) and non-metric multidimensional scaling with Akaike Information Criteria adjusted for variance in sample size (AICc). For inference, I use permutational distance-based linear modeling (DistLM; multivariate multiple regression; Anderson et al., 2004; Kraft et al., 2011). For 2017 data, I use Bayesian inverse modeling to generate GPP and ER (Hall et al., 2016).

Results

Analyses of 2018 data are still underway, but here I present some findings from the 2017 field season. Biogeochemical values (defined as parameters

strongly influenced by nutrient uptake and primary production), are shown in Table 2. For simplicity, other geochemical aspects of water chemistry are shown in Table 3 even though alkalinity and pH can vary tremendously depending on photosynthetic and respiration rates.

The values in Tables 2 and 3 compare the three beaver sites to the LTREB sites during spring runoff and late-summer baseflow conditions. The values are averages of all upstream and downstream samples. The signal to noise ratio for longitudinal patterns from upstream to downstream was high in 2017. With some exceptions, beaver sites had higher variances in all parameters than the LTREB sites. Chlorophyll a, as a proxy for primary production, was higher at the beaver sites during both seasons. Similarly, the 2-dimensional stress values in non-metric multidimensional scaling indicates that sites differ biogeochemically from each other (Figure 5), and not always depending on whether they contain beaver.

Distinctions in samples collected above and below the dams were seasonally dependent. In May 2017 under high flow conditions, the biogeochemistry of the three beaver sites, while separate from each other, showed minimal upstream-downstream distinctions. Conversely, at all three LTREB sites, upstream versus downstream conditions differed in biogeochemistry. All LTREB sites differed from one another in spring. On West Blacktail Creek, biogeochemistry of the beaver site differed from its upstream LTREB site in spring.

In August 2017, the situation changed. In beaver

| | | Oxygen Saturation (%) | NO ₂ (mg/L) | NO ₃ (mg/L) | NH ₃ (mg/L) | PO ₄ (mg/L) | Chl a (mg/L) | DOC (mg/L) | Total N (mg/L) |
|--------|--------------|--------------------------|---------------------------|---------------------------|---------------------------|---------------------------|-----------------|---------------|-------------------|
| Beaver | High flow | 91.38 ±7.5 | 1.13 ±0.58 | 26.41 ±8.52 | 0.01 ±0.01 | 0.25 ±0.08 | 9.41 ±0.35 | 4.84 ±0.94 | 0.16 ±0.05 |
| | Base flow | 96.76 ±3.5 | 2.38 ±0.70 | 20.62 ±9.41 | 0.06 ±0.04 | 0.84 ±0.08 | 22.62 ±3.13 | 6.26 ±2.27 | 0.32 ±0.10 |
| LTREB | High flow | 95.92 ±1.1 | BDL na | 13.18 ±5.75 | 0.14 ±0.09 | 0.39 ±0.05 | 7.37 ±1.92 | 4.35 ±0.54 | 0.20 ±0.06 |
| | Base flow | 96.25 ±0.9 | 2.21 ±0.40 | 21.88 ±6.35 | 0.06 ±0.03 | 0.77 ±0.05 | 18.86 ±5.28 | 6.17 ±1.68 | 0.60 ±0.13 |

Table 2. Nutrient-related biogeochemistry of beaver-colonized and LTREB streams, collected in 2017.

| | | Temperature (°C) | Conductivity (µS/cm) | pH | Hardness (as mg CaCO ₃ /L) | Alkalinity (as mg CaCO ₃ /L) |
|--------|--------------|---------------------|-------------------------|------------|--|--|
| Beaver | High flow | 8.63 ±3.45 | 139.55 ±77.89 | 7.96 ±0.13 | 138.67 ±70.82 | 143.00 ±76. |
| | Base flow | 20.14 ±1.74 | 229.37 ±131.47 | 8.40 ±0.06 | 110.33 ±69.85 | 120.67 ±72. |
| LTREB | High flow | 7.45 ±1.11 | 76.23 ±12.44 | 8.01 ±0.15 | 82.00 ±15.72 | 83.00 ±14. |
| | Base flow | 12.82 ±0.56 | 157.24 ±35.36 | 8.35 ±0.08 | 71.33 ±14.68 | 81.00 ±18. |

Table 3. Geochemistry of beaver-colonized and LTREB streams, collected in 2017.

streams, upstream conditions became different from downstream reaches in Crystal Creek and at the Lower Blacktail Creek in samples collected 3 m above the dam. I attribute this distinction to the large pool at that position dominated by a beaver lodge. At West Blacktail Creek water chemistry at the former beaver colony was not different from conditions at the LTREB site. For LTREB sites, upstream and downstream sampling showed clustered biogeochemistry with the exception that conditions 50 m upstream at East Blacktail differed from those near or below the experimental dam.

Table 4 and Figure 6 show the results of isotopic analyses, carbon, and nitrogen content. The most interesting finding is that willow leaves collected off the beaver dams at West Blacktail Creek and Crystal Creek have $\delta^{15}\text{N}$ values that suggest the nitrogen is approximately two trophic levels above nitrogen sources of willows 50 m upstream of the dams.

Nitrogen has likely been reworked through the sediment microbial community or could have come from beaver or bison feces. Bison are common at Crystal Creek but frequent both up and downstream reaches. Based on my limited observations but also the minimal number of bison feces, they are less frequent visitors to the Lower Blacktail Creek.

Conclusions

Relative to my research questions, trends in distinctions between upstream and downstream conditions support the probability that beaver increase the magnitude of nutrients in streams, and thus, that their biologic influence outpaces hydrologic influences of dam building alone (i.e. slowed flow, warmer temperatures). Network modeling is underway, so I cannot yet provide evidence whether or not beaver increase rates of nutrient cycling or increase stream metabolism via feces and import of terrestrial woody

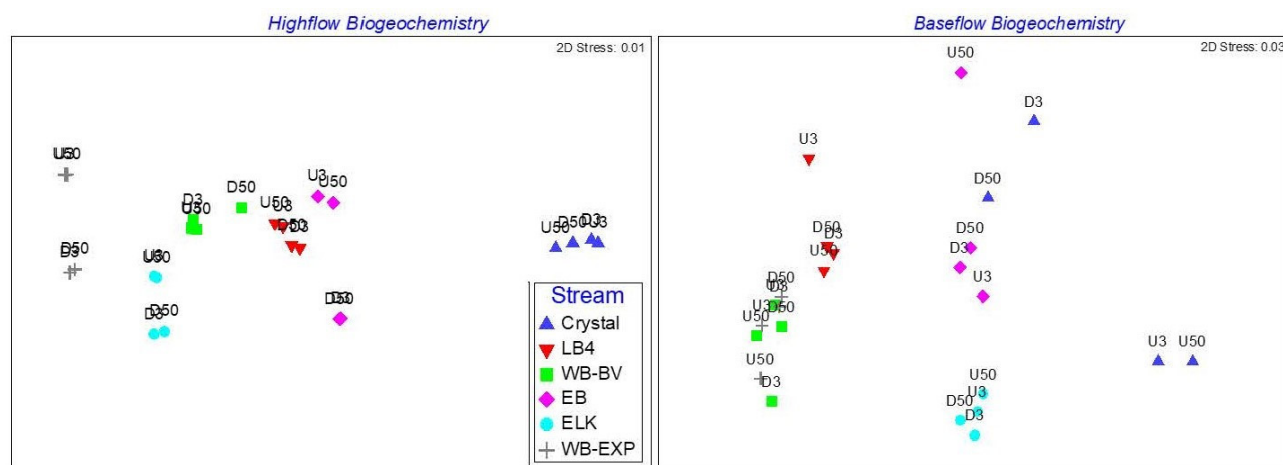


Figure 5. Non-metric multidimensional scaling of biogeochemistry in streams, collected during high flows in May (left panel) and baseflows in August 2017 (right panel). Legend applies to both plots. Crystal, LB4, and WB-BV are sites of beaver dam complexes. EB, Elk, and WB-EXP are experimental LTREB sites **Abbreviations:** U50 or U3 = 50 or 3 m upstream of dams. D3 or D50 = 3 or 50 m downstream of dams. LB4 = Lower Blacktail Creek. WB-BV = Beaver dam complex on West Blacktail Creek. EB = East Blacktail Creek. WB-EXP = LTREB site on West Blacktail Creek. For this analysis, locations at 10 m above and 10 m below dams were excluded because we did not sample for chlorophyll a or DOC and total N at those positions.

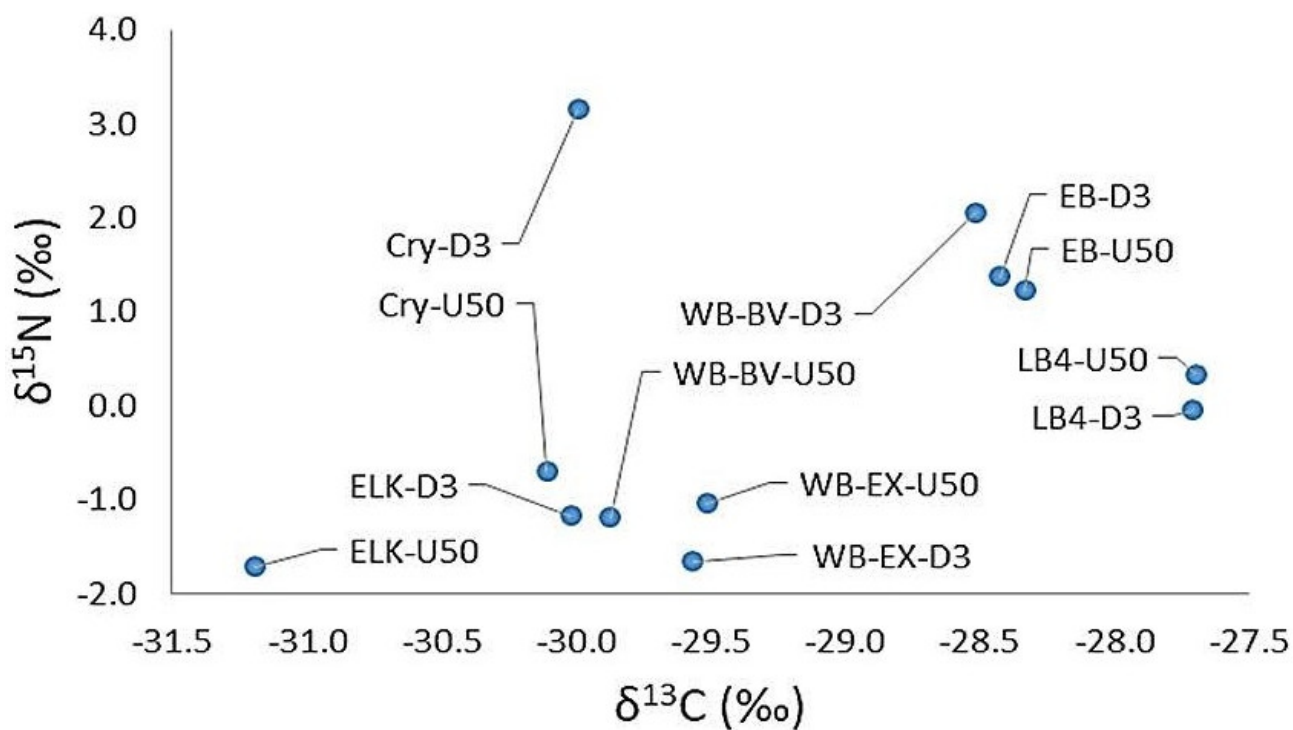


Figure 6. Isotopic signatures in willow leaves collected in August 2017 during baseflow.

| Sample ID | $\delta^{15}\text{N}$ | $\delta^{13}\text{C}$ | Wt% N* | Wt% C* | C:N ratio |
|---------------|-----------------------|-----------------------|--------|--------|-----------|
| CRY-U50-F17 | -0.7 | -30.1 | 1.6 | 45.4 | 28.4 |
| CRY-D3-F17 | 3.2 | -30.0 | 1.6 | 47.2 | 29.6 |
| LB4-U50-F17 | 0.3 | -27.7 | 2.6 | 47.6 | 18.0 |
| LB4-D3-F17 | 0.0 | -27.7 | 1.8 | 47.6 | 25.7 |
| WB-BV-U50-F17 | -1.2 | -29.9 | 2.3 | 46.5 | 20.2 |
| WB-BV-D3-F17 | 2.1 | -28.5 | 2.6 | 48.0 | 18.8 |
| EB-U50-F17 | 1.2 | -28.3 | 2.4 | 47.9 | 19.6 |
| EB-D3-F17 | 1.4 | -28.4 | 2.3 | 48.0 | 20.5 |
| ELK-U50-F17 | -1.7 | -31.2 | 1.8 | 46.9 | 25.8 |
| ELK-D3-F17 | -1.2 | -30.0 | 2.7 | 45.8 | 17.0 |
| WB-EX-U50-F17 | -1.0 | -29.5 | 1.8 | 46.7 | 26.1 |
| WB-EX-D3-F17 | -1.7 | -29.6 | 2.6 | 47.7 | 18.6 |

Table 4. Isotopic and elemental composition data of willow leaves collected in August 2017.

debris. Regarding my final question, "Do beaver contribute significantly to riparian willow and aspen productivity (e.g. shift in stable isotopic signatures)?" $\delta^{15}\text{N}$ values downstream of beaver dams at two sites indicate that the nitrogen likely derives from beaver feces.

Future Work

West Blacktail-Beaver site was included in the 2017 field season because most of the dams remained, and the influence of beaver can continue for several years. This is the second time that beaver abandoned a site and I continued to sample for a year after abandonment. Quantifying how long the beaver signal lasts as colonies blink in and out of the study area is an interesting challenge. Assessing beaver influence on biogeochemistry as it tails off will aid in that challenge. Data needs include:

1. Continue collecting data at the three LTREB sites and three beaver sites per my 2017 research design.
2. To pursue the challenge of identifying the timing and magnitude of beaver influence on state transitions, add a new beaver site that was colonized in summer 2018 (David Cooper, personal correspondence).

3. To assess the potential importance of beaver fecal inputs, conduct targeted isotopic analyses.
4. To improve the noise to signal ratios, conduct time-series measurements of the biogeochemistry over the span of a several days at one representative beaver site and one LTREB. The sampling would be conducted during spring runoff and baseflow.
5. Couple some of the LTREB long-term monitoring with my biogeochemical sampling for greater understanding of state transitions over time as beavers recolonize the Greater Yellowstone Ecosystem.

Acknowledgements

I thank the University of Wyoming-National Park Service for funding in 2017 and for current funding (award # 1003666-SIU). I thank my field assistant, Timothy Knudson for ecological intuition and a strong back. Mr. Lewis Messner, the graduate student who leads the current field research at LTREB sites, provided important logistical information. Dr. David Cooper and Dr. Tom Hobbs have generously provided access to LTREB sites. Conversations with Dr. James Halfpenny and his resources for housing and lab space have been essential to our endeavors.

References

- Anderson, M. J. 2001. A new method for non-parametric multi-variate analysis of variance. *Austral Ecology* **26**:32–46.
- Anderson, M. J., R. B. Ford, D. A. Feary, and C. Honeywill. 2004. Quantitative measures of sedimentation in an estuarine system and its relationship with intertidal soft-sediment infauna. *Marine Ecology Progress Series* **272**:33–48.
- APHA, AWWA, and WEF. 2005. Standard methods for the examination of water and wastewater. 21st edition. American Public Health Association, American Water Works Association, and Water Environment Federation, Baltimore, MD.
- Ayre, K. K., and W. G. Landis. 2012. A Bayesian approach to landscape ecological risk assessment applied to the Upper Grande Ronde Watershed, Oregon. *Human and Ecological Risk Assessment* **18**:946–970. <https://doi.org/10.1080/10807039.2012.707925>.
- Ben-David, M., T. Hanley, and D. Schell. 1998. Fertilization of terrestrial vegetation by spawning Pacific salmon: the role of flooding and predator activity. *Oikos* **83**:47–55.
- Beschta, R. L., and W. J. Ripple. 2013. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade: comment. *Ecology* **94**:1420–1425. <http://dx.doi.org/10.1890/11-0063.1>.
- Collen, P., and R. Gibson. 2000. The general ecology of beavers (*Castor* spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish—a review. *Reviews in Fish Biology and Fisheries* **10**:439–461.
- Creel, S., and D. Christianson. 2009. Wolf presence and increased willow consumption by Yellowstone elk: implications for trophic cascades. *Ecology* **90**:2454–2466.
- Hall, R. O., M. Baker, E. Rosi-Marshall, J. Tank, and J. Newbold. 2013. Solute-specific scaling of inorganic nitrogen and phosphorus uptake in streams. *Biogeosciences* **10**:7323–7331. <https://doi.org/10.5194/bg-10-7323-2013>.
- Hall, R. O., J. L. Tank, M. A. Baker, E. J. Rosi-Marshall, and E. R. Hotchkiss. 2016. Metabolism, gas exchange, and carbon spiraling in rivers. *Ecosystems* **19**:73–86. <https://doi.org/10.1007/s10021-015-9918-1>.
- Helfield, J. M., and R. J. Naiman. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. *Ecology* **82**:2403–2409. [https://doi.org/10.1890/0012-9658\(2001\)082\[2403:eosdno\]2.0.co;2](https://doi.org/10.1890/0012-9658(2001)082[2403:eosdno]2.0.co;2).
- Hossack, B. R., W. R. Gould, D. A. Patla, E. Muths, R. Daley, K. Legg, and P. S. Corn. 2015. Trends in Rocky Mountain amphibians and the role of beaver as a keystone species. *Biological Conservation* **187**:260–269. <https://doi.org/10.1016/j.biocon.2015.05.005>.
- Hubbard Jr, K., L. K. Lautz, M. Mitchell, B. Mayer, and E. Hotchkiss. 2010. Evaluating nitrate uptake in a Rocky Mountain stream using labelled ¹⁵N and ambient nitrate chemistry. *Hydrological Processes* **24**:3322–3336.
- Johnston, C. A., and R. J. Naiman. 1987. Boundary dynamics at the aquatic-terrestrial interface: the influence of beaver and geomorphology. *Landscape Ecology* **1**:47–57. <https://doi.org/10.1007/bf02275265>.
- Johnston, C. A., and R. J. Naiman. 1990. Aquatic patch creation in relation to beaver population trends. *Ecology* **71**:1617–1621. <https://doi.org/10.2307/1938297>.
- Jonas, R., 1955. A population and ecological study of the beaver (*Castor canadensis*) of Yellowstone national park. Master's thesis, University of Idaho, Moscow, ID.
- Kauffman, M. J., J. F. Brodie, and E. S. Jules. 2010. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. *Ecology* **91**:2742–2755. <https://doi.org/10.1890/09-1949.1>.
- Kauffman, M. J., J. F. Brodie, and E. S. Jules. 2013. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade: reply. *Ecology* **94**:1425–1431.
- Klotz, R. 1998. Influence of beaver ponds on the phosphorus concentration of stream water. *Canadian Journal of Fisheries and Aquatic Sciences* **55**:1228–1235. <https://doi.org/10.1139/cjfas-55-5-1228>.
- Kominoski, J. S., A. D. Rosemond, J. P. Benstead, V. Gulis, J. C. Maerz, and D. W. Manning. 2015. Low-to-moderate nitrogen and phosphorus concentrations accelerate microbially driven litter breakdown rates. *Ecological Applications* **25**:856–865. <https://doi.org/10.1890/14-1113.1.sm>.
- Kraft, N. J. B., L. S. Comita, J. M. Chase, N. J. Sanders, N. G. Swenson, T. O. Crist, J. C. Stegen, M. Vellend, B. Boyle, M. J. Anderson, H. V. Cornell, K. F. Davies, A. L. Freestone, B. D. Inouye, S. P. Harrison, and J. A. Myers. 2011. Disentangling the drivers of beta diversity along latitudinal and elevational gradients. *Science* **333**:1755–1758. <https://doi.org/10.1126/science.1208584>.
- Law, A., F. McLean, and N. J. Willby. 2016. Habitat engineering by beaver benefits aquatic biodiversity and ecosystem processes in agricultural streams. *Freshwater Biology* **61**:486–499. <https://doi.org/10.1111/fwb.12721>.

- Marshall, K. N., D. J. Cooper, and N. T. Hobbs. 2014. Interactions among herbivory, climate, topography and plant age shape riparian willow dynamics in northern Yellowstone National Park, USA. *Journal of Ecology* **102**:667–677. <https://doi.org/10.1111/1365-2745.12225>.
- Marshall, K. N., N. T. Hobbs, and D. J. Cooper. 2013. Stream hydrology limits recovery of riparian ecosystems after wolf reintroduction. *Proceedings of the Royal Society B: Biological Sciences* **280**:7. <https://doi.org/10.1098/rspb.2012.2977>.
- Naiman, R. J., and J. M. Melillo. 1984. Nitrogen budget of a subarctic stream altered by beaver (*Castor canadensis*). *Oecologia* **62**:150–155. <https://doi.org/10.1007/bf00379007>.
- Naiman, R. J., G. Pinay, C. A. Johnston, and J. Pastor. 1994. Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. *Ecology* **75**:905–921. <https://doi.org/10.2307/1939415>.
- Painter, L. E., R. L. Beschta, E. J. Larsen, and W. J. Ripple. 2015. Recovering aspen follow changing elk dynamics in Yellowstone: evidence of a trophic cascade? *Ecology* **96**:252–263. <https://doi.org/10.1890/14-0712.1.sm>.
- Persico, L., and G. Meyer. 2013. Natural and historical variability in fluvial processes, beaver activity, and climate in the Greater Yellowstone Ecosystem. *Earth Surface Processes and Landforms* **38**:728–750. <https://doi.org/10.1002/esp.3349>.
- Raiho, A. M., M. B. Hooten, S. Bates, and N. T. Hobbs. 2015. Forecasting the effects of fertility control on overabundant ungulates: white-tailed deer in the National Capital Region. *PLoS ONE* **10**:24. <https://doi.org/10.1371/journal.pone.0143122>.
- Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? *BioScience* **54**:755–766.
- Ripple, W. J., and R. L. Beschta. 2012. Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. *Biological Conservation* **145**:205–213. <https://doi.org/10.1016/j.biocon.2011.11.005>.
- Roe, A. M., C. B. Meyer, N. P. Nibbelink, and M. Ben-David. 2010. Differential tree and shrub production in response to fertilization and disturbance by coastal river otters in Alaska. *Ecology* **91**:3177–3188.
- Schook, D. M., and D. J. Cooper. 2014. Climatic and hydrologic processes leading to wetland losses in Yellowstone National Park, USA. *Journal of Hydrology* **510**:340–352. <https://doi.org/10.1016/j.jhydrol.2013.12.038>.
- Warren, E. R. 1926. A study of beaver in the Yancey region of Yellowstone National Park. *Roosevelt Wild Life Annals* **1**:13–191.
- Wolf, E. C., D. J. Cooper, and N. T. Hobbs. 2007. Hydrologic regime and herbivory stabilize an alternative state in Yellowstone National Park. *Ecological Applications* **17**:1572–1587. <https://doi.org/10.1890/06-2042.1>.